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XIX.—*On the Original Form, Development, and Cohesion of the Bones of the Sternum of Chelonians; with Notes on the Skeleton of Sphargis.* By Dr. J. E. GRAY, F.R.S. &c.

[Plates IV., V., & VI.]

It has long been known that the sternum of all Chelonians is formed of four pairs of bones with an odd one, which is always attached to the centre of the inner edge, opposite the suture between the front pair. In some Chelonians these bones always remain of nearly the same form, and are more or less separate from each other during the whole life of the animal. In the land Tortoises and the freshwater Tortoises or Terrapins the bones of the young become expanded as the animal grows, coalesce, and at length form in the adult animal a single bony disk.

Cuvier, in his chapter on the “Ostéologie des Tortues,” in the *Oss. Foss.* v. p. 204, observes:—

“Dans les tortues de terre et d'eau douce, et dans les chélydes, ils ne laissent de vides entre eux que dans le premier âge seulement, où ils se forment de rayons osseux dirigés en divers sens dans le disque encore cartilagineux du plastron, comme les os du crâne dans les fétus des mammifères; mais avec l'âge ces rayons se joignent de toute part et forment un disque compact dans toutes ses parties et qui s'unit par une étendue plus ou moins considérable de chaque côté au bouclier dorsal. Voyez pl. xii. f. 44, le plastron d'un jeune *Testudo scabra.*”

The sternum figured is very like that here figured as belonging to *Emys concentrica*, and is quite different from that of
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T. scabra of Latreille, which is figured here under the name of *Rhinoclemmys scabra*. Mr. Owen figures the skeleton of a young *Testudo indica* 'Phil. Trans.' cxxxix. 1849, t. 19. f. 4-6. These are the only observations I have noticed on the form of the bones in the sternum of the young Chelonians. These authors did not seem to be aware of the great variation in the forms of the bones in the young of the different genera, the changes that they undergo during the growth of the animal, and the important assistance that their study affords in the arrangement of the animals.

Land-Tortoises (Testudo).

The bones of the sternum in young Land-Tortoises (*Testudo*) are the same in number as in the Terrapins, but of very different form. The front two pairs and the hinder two pairs each form a very distinct group, separated by a more or less broad space across the middle of the sternum. The front pair of bones are generally large and well developed, and the odd bone on the inner side of them is triangular and usually small. The two lateral pairs are somewhat similar, broad and expanded, and more or less semilunar, each pair having a convex semi-circular edge towards the middle of the inner central vacant disk. The hinder pair are attached to the inner side of the outer edge of the hind lateral pair, and are generally united together.

This formation is well exhibited in a specimen of *Testudo tabulata* (Pl. IV. fig. 1) $2\frac{1}{2}$ inches long, and also in a specimen of *T. elephantopus* (Pl. IV. fig. 2), about 4 inches long, and *Testudo radiata*, $2\frac{1}{2}$ inches. The lateral bones in *Testudo radiata* and in *T. indica* are much more convex and irregular on the edge towards the centre of the sternum.

In *T. platynota* (Pl. IV. fig. 3), about 2 inches long, the lateral bones are of the same lunate shape as in *T. tabulata*, but the lateral pair are much further apart. Perhaps this arises from the ossification being less developed. The lateral bones in *T. semiserrata*, about 2 inches long, are similar to those of the young *T. tabulata*, but rather more irregular in their outline; but the opposite bones are rather further apart, leaving a broader central space between them than in *T. tabulata*.

These bones evidently enlarge in size, their edges approximate, and at length join and coalesce. Thus *T. stellata* (Pl. IV. fig. 4) appears to become solidified when of a very small size; for in a specimen only 2 inches long the ribs are dilated and ossified nearly to the margin, and the sternal bones are very expanded, forming a nearly solid disk, leaving only

a broad rhombic vacant space not quite half the width of the sternum; and in a specimen $2\frac{1}{2}$ inches long, this vacant space is reduced in size so as not to be a third of the diameter of the disk. But I think it is very probable that in the very young of this species the separate bones of which the sternum is composed are all more dilated than in the other species, although I have no specimens by which I can indicate this fact.

Freshwater Tortoises or Terrapins.

The sternum of the young Freshwater Tortoises is composed of the same number of bones (which are united together into a bony disk in the adult animal) as that of the Land-Tortoises; but these bones are very different in shape and disposition from those of the Land-Tortoises, and differ in the various groups, offering a curious subject of study.

The sterna of the adult animals are naturally divided into three groups:—

1st. The sternum solid, continuous, and firmly connected with the marginal and other bones of the dorsal disk by an ascending lateral process from each of the central lateral pair of bones.

2nd. The sternum is only connected with the marginal plates of the dorsal disk by a cartilaginous suture or an adhesion between the bones of the sternum and the marginal plates. These are called Box Tortoises.

The Box Tortoises present two forms:—

In the *true* Box Tortoises the sternum is divided transversely into two portions, which close down on the cavity of the upper shell before and behind. The suture is about the middle, between the two lateral bones—the front lobe consisting of the anterior and anterior lateral bones, and covered externally by the gular, pregular, and pectoral plates, the hinder portion consisting of the hinder lateral and the hinder sternal bones. It is covered externally by the abdominal, preanal, and anal shields.

In the Trap Tortoises the sternum is divided into three portions by two transverse sutures. The middle one, which consists of the anterior and posterior lateral bones (which form a square central portion), is attached by a cartilaginous or more or less bony suture to the margin of the dorsal shield, and does not send any ribs up to the inner part of it. It is covered by two large abdominal shields. The front flap consists of the frontal pair of bones and the odd bone; the front pair are very much larger than usual. It is covered by the gular plates (which are generally soldered into one) and the intergular and pectoral plates (which are triangular). The hinder flap only consists

of the hinder pair of bones, which are much larger than usual, and united by a straight median suture; it is covered by the preanal and anal plates.

This form is described from the genera *Swanka* and *Kinosternon*, where this modification of the sternum is in its most developed state. The sternum of the other genera is often narrow, and a portion is only slightly mobile, and the plates (which cover it) are diminished in number or coherent together.

The land-tortoise *Pyxis* and the fluviatile *Sternotherus* have the front lobe of the sternum free; but it is only the front lobe of the sternum that is free, the abdominal portion being firmly united to the marginal portion of the back, as in the tortoises with an undivided sternum.

The true Box Tortoises consist of the family Cistudinidæ.

The Trap Tortoises consist of the Chelydradæ.

3rd. All the other families of Freshwater Tortoises or Terapins have a simple undivided sternum.

One might premise that these three forms would each have a distinct development of the bones of which the sternum is formed, or that the bones of each of the three forms would be of the same shape and developed in the same manner during the growth of the animal. But the examination of the young specimens which have come under my observation (which, unfortunately, are too few for the proper study of the subject) proves this not to be the case; and I am inclined to think that the study of the development of these bones may be subservient to the natural arrangement of these animals, and also a great assistance in the determination of the fossil species.

The development of bones of the sternum of Freshwater Tortoises may be divided into three series, thus:—

I. The nine bones in the very young state are well developed, the lateral bones being largely developed and covering the greater part of the middle of the sternum. There is a moderate-sized vacant space in the middle of the sternum, and a smaller one at the hinder part of the sternum, between the inner hinder angles of the lateral pair of bones and the inner side of the hinder plates, and an oval space on each side of the angular odd bone between it and the inner front edge of the anterior lateral bone.

This form is well exhibited in the sternum of *Malaclemmys concentrica* (Plate V. fig. 1) of the family Malaclemmydæ, and of *Pelomedusa subrufa* (fig. 2), family Hydraspidæ. The anterior lateral bones are larger and more developed in *Malaclemmys* than in *Pelomedusa*; and this appears to be the most usual form of the sternum of the Freshwater Tortoises.

In *Chelydra serpentina*, even when the shell reaches 7 inches length, the sternum is not united along the central longitudinal suture, and there is a triangular cavity on each side of the narrow lanceolate odd bone and the front end of the front lateral, and a moderate-sized square unossified portion between the inner ends of the front and hinder lateral bones on the suture between the pectoral and abdominal plates.

The sternum of the skeleton of the young *Stauremys Salvini* in the British Museum is like that of *Chelydra*; but the inner edge of the front bones is further apart, and the odd sword-shaped bone is thinner and longer.

II. In the second form the four pairs of bones form a ring round the margin of the sternum, the two pairs of lateral bones being the least developed and forming the narrowest part of the ring, leaving a large open space in the centre between all the bones which form the greater part of the sternum, with the point of the odd bone projecting into it. This form is well seen in the sternum of *Cyclemys dhor* (figs. 3), belonging to the family Cistudinidæ.

Rhinoclemmys scabra (fig. 4). As this animal grows, the front part of the sternum becomes more dilated and extended externally on the front of the outer side. It is also to be observed in the animal that I have described and figured as *Emys pulcherrima* (Cat. Sh. Rept. pl. xxv. fig. 1), which may be a *Rhinoclemmys*. These two latter terrapins belong to the family Emydidæ.

III. This form is somewhat intermediate between the two former. The four pairs of bones in the young animal are even less developed, and form only a narrow ring round the margin of the sternum, leaving a very large part of the sternum only formed of membrane, occupying more of its space than even in the former kind; but the anterior lateral and posterior lateral bones throw out each a more or less narrow bony process across the space, dividing it into three portions. Into the front edge of the front one the small triangular odd bone projects. In *Notochelys platynota* (Pl. IV. fig. 5) the front pair of bones is moderate. The inner process of the front pair of lateral bones is small, but broad and divided into three or four finger-like lobes at the end. This belongs to the family Cistudinidæ.

In *Kachuga* (Pl. VI.) the front pair of bones is less developed. The inner lobes of the front lateral pair of bones are, as in the former, broader and divided into finger-like lobes at the end. The internal bony lobes of the hinder lateral bones are well developed, and like those of the front pair of bones, but much narrower; but, unlike the sternum of *Notochelys*

(Pl. IV. fig. 5), the hinder pair of bones are not united together behind, and each sends forth a lobe from the middle of the inner side, which eventually unite in the centre line, leaving a small posterior central space between the hinder ends of these bones.

This form seems common and perhaps peculiar to the family Bataguridæ. I have figured the inside of the sternum of a very young specimen of *Kachuga major* (Pl. VI. fig. 1), which has the bones and lobes very slender. These parts are more developed in *Kachuga dentata* even in the youngest state, the outside of which is figured (fig. 2), and which has the posterior pair of bones; and in an older specimen in the British Museum this is also figured from the outside.

In *Morenia* and *Pangshura* the hinder part of the sternum is ossified soonest if these vacant spaces exist in the very young specimens.

In the young *Morenia Berdmorei*, about 4 inches long, there is an oblong longitudinal unossified space on each side between the branches of the sternum and the margin, and an elongate four-sided space in the centre between the sutures of the pectoral and abdominal plates, and another rather smaller one between the preanal plates. There is a series of large spaces between the ends of the ribs and the marginal bone.

In a skeleton of a half-grown *Pangshura tecta* there are two rhombic imperfections, the one placed between the sutures of the pectoral and abdominal plates, and a rather smaller one between the two preanal plates.

This form bears some relation to the bones found in a very young *Chelonia* (Pl. VI. fig. 4), where the anterior bones are very narrow. The anterior and posterior lateral bones of each side are separate from each other, having a simple rounded end; each of them has two digitate external lobes, extending towards the margin of the dorsal disk: the anterior one has two simple processes towards and uniting at the centre; the hinder one has a series of simple digitate processes extending towards the centre and hinder part of the sternum.

Another form is very peculiar; and as yet I have only seen one example, in a very young specimen of *Elseya dentata* (Pl. V. fig. 5), belonging to the Hydraspidæ, from Australia. The front pair of bones, the odd bone, and the front lateral bones are all united together and form a solid front half to the sternum. The hinder lateral bones and the hinder pair of bones are narrow, and form a margin to the hinder half of the sternum, leaving a very large triangular central space. In an older specimen the large naked space becomes filled up, except a very small oblong hole in the middle of the suture of the preanal plates, and a

larger roundish subhexagonal open space occupying the place of the suture between the abdominal plates.

Perhaps a somewhat similar structure exists in the young *Hydromedusa flavilabris* (Pl. VI. fig. 3); but I have only been able to examine and figure the outside of this specimen, and have not described the separate bones of which it is composed. But this form does not seem to be universal in the Hydraspidæ, as in the young *Chelymys Victoriae* in the British Museum (about five inches long), examined from the outside, there is a narrow rhombic unossified space in the suture between the pair of abdominal plates, and a narrower lanceolate space between the hinder part of the preanal plates, somewhat like what we find in the young Bataguridæ.

Thus it will appear that the tortoises that have a solid continuous sternum in their adult state have the bones of which it is composed of a very different form in their young state, though they are all developed into a solid mass composed of nine bones in the adult state, as, for example, *Malaclemmys* (Pl. V. fig. 1) of Malaclemmydæ, *Pelomedusa* (fig. 2) of Pelomedusidæ, *Chelydra* and *Stauremys* of Chelydradæ, *Kachuga* (Pl. VI. figs. 1 & 2), *Morenia*, and *Pungshura* of Bataguridæ, *Rhinoclemmys* (Pl. V. fig. 4) of Emydidæ.

Thus, among the Box Tortoises, the sternum of the young *Cyclemys dhor* (Pl. V. fig. 3) is very like that of *Rhinoclemmys*, and the young of *Notochelys platynota* is like that of *Batagur*. We have not had the opportunity of examining the young state of the other genera of Box Tortoises.

I labour under the same disadvantage with regard to the young state of the two-flapped Trap Tortoises. I have only seen the young stuffed specimen of *Kinosternon pennsylvanicum* (Pl. V. fig. 6), which I can only examine from the outside. That has an oblong slender unossified space occupying more than half the length of the central suture of the sternum, somewhat like, but narrower than, the unossified space of *Cyclemys* and *Rhinoclemmys*.

Mud-Tortoises (Trionyx).

The bones of the sternum of the young and adult Mud-Tortoises undergo little alteration of shape; only the adult animals have on the outer surface of each an expanded bony callosity, which, like those on the outer surface of the ribs, is pitted externally and covered with a soft skin, so that the expansions of the ribs and sternal bones are only seen in the animal when it is dry. They are peculiar for having the first pair of sternal bones elongate and bent like an L, one branch of each being directed straight forward, and the clongate

odd bone, on the inner margin of the other branch, slightly arched.

In some genera there is only in the adult state a callosity on the sides next the suture between the two middle pairs of bones, as *Aspilus*; in others these callosities are expanded, as in *Rafetus*; but generally the anal pair of bones are also covered with expanded callosities, as in *Trionyx*. In some, as *Emyda*, the front pair and the odd front bone are provided with callosities. The Mud-Tortoises are generally without any bones on the margin; but some few bones are developed in the margin of the adult animal in *Emyda*.

The development of the genus *Emyda* has been imperfectly observed. In *E. punctata* the margin of the disk of the young is flexible, without any marginal bones. At length an oblong marginal bone is developed on the front part of the hinder side over the hind legs; and afterwards a series of smaller marginal bones are developed on the margin behind it. When very young the expanded bony dorsal disk is very narrow, only occupying the centre of the back, the expanded part being shorter than the ribs.

The odd front bone is rather broader than long, and separated from the front pair of bones by the prominent square first vertebral callosity; but as the animal grows the odd first callosity becomes much broader and closely united to the first pair of callosities, which become wider so as quite to enclose the first vertebral callosity. It is not until after this change has taken place that the single anterior nuchal callosity and the two hinder lateral callosities before referred to, over the hind feet, are developed. At length the anterior transverse callosity is united to the front of those of the first pair of ribs to form the dorsal shield, and the single anterior marginal callosity fits into a central notch in its front margin.

In the young specimen the odd anterior marginal callosity is not developed. When the three marginal bones before mentioned are developed, then it is oblong, transverse, and very small; but it enlarges as the animal increases in size.

In the very young specimen the front pair of sternal callosities are small, roundish, and very far apart. They gradually increase in size, being at first rounded quadrangular, rather longer than broad; but they at length spread out on the sides, and are much broader than long, being broader in front than on the outer side. The hinder pair of sternal callosities are always separate behind. In the very young specimens the pair are far apart, much longer than broad, arched on the inner and straight on the outer side. As they increase in size they become broader compared with their length, and closer together,

and at length irregularly semicircular, rather longer than broad, nearly close together, and oblique to each other.

The other species (*E. ceylonensis*), when adult, has the hinder pair of callosities subquadrangular, parallel, and nearly united by a straight inner edge and a large rounded anterior callosity.

Sea-Turtles.

The number of the sternal bones of Turtles is the same, and the first pair and the odd bone on the inside of them are of the same form, as in the Terrapins; but they always remain more or less separate from one another, and do not enlarge, solidify, and consolidate into a continuous bony disk.

As in the Terrapins, the bones of the sternum in the young Turtles are found in two forms. In the true Turtles (*Chelonia*) (Pl. VI. fig. 4) the three hinder pairs of lateral bones are always expanded and furnished with radiating lobes on the inner and outer edges. These lobes are very uniform in their direction and generally in their form, and afford very good characters for the distinction of the species and their division into groups. In the Luth (*Sphargis*) (Pl. VI. fig. 5) the sternal bones in the young state are very narrow, cylindrical and weak, merely forming a slight framework to the circumference of the sternum, and the two front pairs form a group which is separated by a considerable space on the side of the sternum from the part of the ring formed of the two hinder lateral pairs, being in this respect somewhat like the sternum of the young Land-Tortoises, but consisting of slight cylindrical rudimentary bones instead of the broad expanded ones of that group.

The study of the development of the sternum of the tortoises has brought out affinities between groups that have not hitherto been observed; and no doubt, as the state of the bones in more young specimens is known, it will greatly add to our knowledge of the relations which the genera bear to each other. This may be exhibited by the following table, which will lead the zoologist and comparative anatomist to consider this subject, and see many affinities between groups that have hitherto been considered very different, and divergences in groups that have hitherto been regarded as allied.

Chelonians may be divided thus:—

- I. The bones of the sternum, and also of the dorsal disk and margin, of the adult animal all united together and consolidated as if they were a single bone.
 - a. The bones of the sternum in the young animal expanded,

and forming a more or less bony disk protecting the greater part of the sternum.

* The sternal bones in the very young expanded and forming two groups:—the front, of the two anterior pairs of bones and the odd bone; the hinder, of the two hinder pairs of bones, leaving a space in the middle of the sides. *Tylopoda* or Land-Tortoises: *Testudo* &c.

** The sternal bones of the very young united into a disk or marginal ring. *Steganopoda* or Terrapins, as *Malaclemmys*, *Pelomedusa*, *Chelydra*, and *Staurotypus*.

It is to be observed that it is among the latter genera of the family Chelydradae that the sternum of these animals is smaller and less developed compared with the size of the animal than in any other Chelonians.

b. The bones of the sternum in the young animal slender, and merely forming a ring round the circumference of the sternum, leaving the centre part vacant, to be filled up by the development of the bones.

In the most developed form of this group the bones form a simple external ring, leaving the centre of the disk vacant, as in the genus *Rhinoclemmys* among the Terrapins with a continuous sternum, and *Cyclemys* among the Box Tortoises (which have the sternum divided into two parts by a central suture); and the structure seems to be similar in the genus *Kinosternon* (Pl. V. fig. 6), which have the sternum divided into three parts by two cross sutures, and have been called Flap-Tortoises.

Some of the tortoises that have the sternum in the very young state supported by a ring of bones send forth bony lobes from the inner side of the three pairs of lateral bones, which divide the vacant central space into four parts; this has only been observed in the genus *Kachuga* among the Asiatic Batagurs. This group is intermediate between the two sections *a* and *b*; and the sternum of the young has considerable affinity to the sternum of the adult turtles.

II. The bones of the sternum in the adult animal remaining separate, and only forming a ring of bones round the centre part of the disk.

In the marine Turtles the marginal bones are only slightly developed; and in the freshwater Mud-Tortoises the marginal bones are not developed at all, or only deposited on part of the margin when the animal arrives at the adult age. These may be divided into:—

The Mud-Tortoises (*Trionychidæ*). The front pair of sternal bones separate, slender, bent at a right angle in the middle,

the front part produced forwards, the hinder to the side, and attached on the inner side to the elongate arched odd bone.

The Turtles (*Chelonia*) have the front and hinder pairs of bones narrow, and the front pair furnished with an elongate, more or less lanceolate, odd bone at the posterior end of the suture between the front pair.

* The two lateral pairs of sternal bones being expanded and more or less united in the Turtles.

** The two lateral pairs of sternal bones linear and far apart in the Luth.

The Mud-Tortoises and the Luth are peculiar among tortoises for being covered with a soft leathery skin instead of the horny plates peculiar to this group of animals: but the Mud-Tortoises have beneath their skin more or less dilated callosities, forming their ribs and sternum into a solid mass; while in the Luth the ribs and sternal bones are very slightly developed, separate from each other, being chiefly supported by the hard callosities enclosed in the skin, so that it may be regarded as a reptile on the border of the vertebrate kingdom.

On the Osteology of Sphargis &c.

In the adult *Sphargis* the bones are not more developed, considering the size of the animal, than they are in the very young (previously described), and very unlike the skeleton of other Chelonians. There is no regular dorsal or sternal shield, nor marginal bones. The vertebræ are compressed; the seven ribs on each side are depressed, weak, of nearly the same width the whole length, and quite separate from each other, and without any bony expansion between them to form a dorsal disk as in other Chelonians. In all the other very young tortoises I have seen, the ribs are lanceolate, more or less dilated near the vertebral column; and it is from the upper surface of this dilatation that the callosities of the outer surface by which the ribs are united commence and gradually proceed down the ribs to the marginal bones.

The sternum of the adult specimen (5 feet long) examined was more rudimentary and less apparent than in the very young specimen about 4 inches long, which is figured in Pl. VI. fig. 5.

The animal, unlike the generality of Chelonians, appears to be chiefly supported by its hard, longitudinally costate skin. The skin is very thick, and the whole outer surface is studded with very close hard hexangular disks, more like the surface of a trunkfish (*Ostracion*) than any thing that I can compare it with. These disks are larger and more oblong on the

longitudinal ridges of the back, the sides of the sternum, and on the sides of the tail, and are produced above into hard conical elevations or tubercles, which are largest on the ridges of the tail. These tubercles are somewhat like those to be observed on some species of *Ostracion* and on *Lophius* and other fishes.

The form of the two hinder central bones of the dorsal disk (placed beyond the one that bears the pelvis, and forming the central line of the hinder part of the shell that covers the tail of the animal) is very different in the young and halfgrown specimens of the different kinds of turtles, and affords a very good character to determine the species; but these bones expand in the more adult state when the dorsal shell becomes solidified by the dilatation and coherence of the ribs, when they lose the distinctness of their form, or at least they become coalesced with the other bones and are not to be observed.

Thus in the young *Caouana* the hinder bone is narrow and compressed, with a prominence on its outer side; in the other turtles this bone is flat and expanded. In the Green Turtle (*Mydas*) the last bone is lanceolate, ovate, and broad at the base, and slightly contracted at the front edge, and the hinder part is gradually contracted into a point. The last bone of the Hawk's-beak (*Caretta*) is similar, but broader and more rapidly attenuated behind, and not contracted in front next to the pelvis.

EXPLANATION OF THE PLATES.

PLATE IV.

- Fig. 1.* Testudo tabulata.
Fig. 2. Testudo elephantopus.
Fig. 3. Testudo platynota.
Fig. 4. Testudo stellata.
Fig. 5. Notochelys platynota.

PLATE V.

- Fig. 1.* Malaclemmys concentrica.
Fig. 2. Pelomedusa subrufa.
Fig. 3. Cyclemys dhor.
Fig. 4. Rhinoclemmys scabra.
Fig. 5. Elseya dentata.
Fig. 6. Kinosternon pennsylvanicum.

PLATE VI.

- Fig. 1.* Kachuga major.
Fig. 2. Kachuga dentata (outside).
Fig. 3. Hydromedusa flavilabris (outside).
Fig. 4. Chelonia mydas.
Fig. 5. Sphargis mercurialis.